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Unlike rolling stones: not every *Myrmecina* species actively rolls away from danger (Hymenoptera, Formicidae)

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Abstract
Actively rolling away is a very rare escape strategy in the animal kingdom, which to date has only been documented in a few arthropod and one vertebrate species. One of these arthropods is a West-Palearctic ant, *Myrmecina graminicola*, which has very recently been demonstrated to actively curb into a ball-like shape rolling away upon disturbance, and to selectively display this behavior only under particular circumstances. We tested whether one of the other three W-Palearctic *Myrmecina* species, the rare insular endemism *M. sicula*, exhibited the same behavioral response, using the same experimental approach used for *M. graminicola*. Our results showed that *M. sicula* reacted to moderate disturbance by either freezing its body or walking away. Only when the individual lost contact with the substratum, it could curl into a ball-like shape, yet this was significantly less refined than the one displayed by *M. graminicola*, as the appendages of *M. sicula* are not tightly kept close to its body. However, *M. sicula* never performed the active rolling behavior that is readily exhibited by *M. graminicola*. Ecological, morphological, and phylogenetic constraints may have determined the lack of a developed active rolling escape-strategy in *M. sicula*. Further investigations are required to assess the presence or absence of this unique behavior across *Myrmecina* lineages.

Keywords: *Escape strategies, ant behavior, insular endemism, Mediterranean ants*

Introduction

Arthropods developed a wide range of mechanical, chemical and behavioral defensive strategies that appear fundamental to their success (Pasteels et al. 1983; Eisner et al. 2005). Among them, several adaptations are aimed at avoiding the danger rather than counterattacking, which can be more cost-effective, according to the circumstances (Buschinger & Maschwitz 1984; Visicchio et al. 2001; Langerhans 2007). Like other social arthropods, ants can exhibit a variety of defensive responses at the individual or collective level, from fighting to avoidance or escaping (Hölldobler & Wilson 1990). Among escaping strategies, some require particular adaptations and are remarkably typical of only a handful of species. Good examples are the jumping ability of the genera *Harpegnathos* Jerdon, 1851, *Gigantiops* Roger, 1863 or *Odontomachus* Latreille, 1804 (Ali et al. 1992; Wheeler 1922; Spagna et al. 2009), the gliding ability developed by *Cephalotes* Latreille, 1802 ants (Yanoviak et al. 2005). However, the recently described case of a context dependent "rolling away" ability in the ant genus *Myrmecina* Curtis, 1929 represents an even rarer strategy that compares with only a handful of other cases in the whole animal kingdom. Workers of the West-Palearctic *Myrmecina graminicola* (Latreille, 1802) are able to curb into a ball and roll away at remarkable speed upon disturbance (about 40 cm/s under experimental conditions), and they do so only if disturbed on a surface with an inclination of at least 25° (Grasso et al. 2020). The few animals which are known to employ a similar strategy of actively rolling away from danger are spiders from the genus

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Carparachne Lawrence, 1962 (Araneae: Sparassidae), caterpillars of *Pleuroptya ruralis* (Scopoli, 1763) (Lepidoptera: Crambidae), the stomatopod *Nannos quilla decemspinosa* (Rathbun, 1910) (Stomatopoda: Nannosquillidae) and the Mount Lyell salamander *Hydromantes platycephalus* (Camp, 1916) (Urodela: Plethodontidae) (Caldwel 1979; Henschel 1990; Full et al. 1993; García-París & Deban 1995; Brackenbury 1997). The rolling strategy of *M. graminicola* is thought to allow it to perform very rapid short-range movements within the different microhabitats where these ant forage, above and within the upper soil (Grasso et al. 2020).

Contrary to several other myrmicine ants that form very populous colonies, and sometimes large or even permanent foraging trails (see Hölldobler & Wilson 1990; Grasso et al. 1998, 1999; Steiner et al. 2011; Seifert 2018), *Myrmecina* ants live in relatively small societies and forage solitarily or in small groups (Seifert 2018). The evolutionary relationships within the genus *Myrmecina* are still unclear, as no global phylogeny exists. The diversity of the genus is largely concentrated in South-Eastern Asia and Oceania, but a handful of species are distributed across the Holarctic region (Janicki et al. 2016; Guénard et al. 2017). The biology of most *Myrmecina* species is very little known, and even if *M. graminicola* is one of the few relatively well-studied exceptions (e.g. Donisthorpe 1927; Buschinger & Schreiber 2002; Buschinger et al. 2003; Buschinger 2003, 2005; Seifert 2018), its remarkable escaping behavior was discovered only recently (Grasso et al. 2020). It is therefore possible that other *Myrmecina* species share with *M. graminicola* the same anti-predatory strategy.

Myrmecina sicula André, 1882 is one of the three species of the West-Palearctic *M. sicula* complex and lives sympatrically with *M. graminicola* in a narrow geographic range in the North-Western sector of the large Mediterranean Island of Sicily (Italy) (Schifani et al. 2020). The identity of this taxon has long been obscure until recently, and many of its fundamental biological traits remain undocumented (Schifani et al. 2020). The evolutionary relationship between *M. graminicola* and the *M. sicula* complex is still unknown, but together they represent the entirety of the West-Palearctic *Myrmecina* species (Rigato 1999; Schifani et al. 2020). Here, we attempted to test whether the rolling behavior described by Grasso et al. (2020) in *M. graminicola* is also displayed by *M. sicula*.

Materials and methods

Methodologies followed Grasso et al. (2020), whose experiments were replicated with a different ant species. Experiments were conducted on 10 ants from 5 *M. sicula* colonies originating from 4 sites in the Palermo province (Sicily, Italy). The number of replicas was constrained by the cryptic habits of this species which make sampling efforts difficult (see Schifani et al. 2020). Ants were temporarily kept in small test tubes with moist soil, and every ant underwent 2 different tests, named the *Sloped Plane Test* and the *Horizontal Plane Test*, each consisting of multiple trials. However, each individual was subject to a trail only once every 2 days to avoid excessive stress.

As in Grasso et al. (2020), we aimed to expose *Myrmecina* workers to a gradient of disturbances, providing vibrational stimuli of variable intensity or causing the ants to lose contact with their substratum in order to elicit a defensive response. The reason to make separate tests on both a sloped plane at different inclinations and on an horizontal plane lay in the fact that *M. graminicola* only performs its characteristic rolling behavior on sufficiently sloped planes.

In both tests, the occurrence of the following behaviors described in detail by Grasso et al. (2020) were recorded:

- Walking away: the ant walks more than one step away from the source of disturbance.
- Freezing: the ant stops moving, becoming motionless for at least 1.5 seconds.
- Curling: the ant assumes a tight position, displaying a ball-like shape. For this behavior, we also recorded its duration.
- Rolling: the ant curls into a proper ball-like shape and lets itself roll forward, possibly using its antennae and legs to facilitate the movement.

Sloped plane test

A first set of trials aimed to verify the exhibition of rolling behavior by ants that received 2 different stimuli while walking at 10 different plane inclinations (0°, 5°, 15°, 20°, 25°, 30°, 35°, 40°, 45°, 90°). The applied stimuli were:

- Rubbing: slight substrate rubbing, using an entomological forceps, just behind the walking ant while avoiding any contacts with its body;
- Tapping: single slight tap with a plastic stick at the base of the experimental device.

An inclinable plastic plane (5 × 17 cm) covered by filter paper (changed after every trial) with a 3 cm horizontal platform was the experimental setup upon which individual ants were introduced and tested (Figure 1). For each test, we performed 10 replicas for a total of 200 trials (2 stimuli × 10 inclinations × 10 replicas).

Horizontal plane test

A second set of trials was performed to evaluate ant behavioral responses to disturbance on the horizontal plane. Ants were tested using 5 different stimuli:

- Slight substrate tapping: slightly tapping of the horizontal plane by a plastic stick.
- Strong substrate tapping: strongly tapping of the horizontal plane by a plastic stick making the ant bounce (temporarily losing contact with the substratum).
- Slight gaster tapping: lightly tapping on the ant's gaster by the tip of an entomological forceps.
- Strong gaster tapping: strongly tapping on the ant's gaster by the tip of an entomological forceps, causing the ant to temporarily lose contact with the substratum.
- Vertical drop: ants were dropped vertically on the horizontal plane from a height of 10 cm.

The experimental setup consisted in a 10 × 10 cm arena covered with filter paper (changed after every trial). For each stimulus, we conducted 10 replicas, for a total of 50 trials (5 stimuli × 10 replicas).

Results

Sloped plane test

The only behavior we recorded independently from the different degrees of inclination used or from whether rubbing or tapping were the stimuli (see Supplementary Information).

Horizontal plane test

Ants mostly responded by walking away when reacting to slight substrate tapping (80%), while freezing dominated their responses to strong substrate tapping and slight gaster tapping (70–100%). Curling was the most frequently observed reaction to stimuli that implicated a loss of contact with the substratum, namely strong gaster tapping and vertical drop (80–100%; Figure 2).

Curling implies displaying a ball-like position, but in all observations ($N = 20$) this position was only superficially similar to the one described in *M. graminicola* since the legs and especially the antennae of *M. sicula* never perfectly adhered to the body (Figure 3). The rapid standardized retraction of scapi towards capsule, which is a key part of *M. graminicola* behavior, was never observed in *M. sicula*.

The duration of the ball-like position assumed by ants curling their body varied according to the intensity of the stimuli they received. Considering the stimuli that provoked a curling response in >50% of the ants, namely Stronger gaster tapping and Vertical drop (Figure 2), the duration of the ball-like position was significantly longer in the latter (paired t-test: $t_9 = -10.92$, $p < 0.001$; Figure 4).

Discussion

Our experiments allow to make a rather detailed comparison of the behavioral responses to disturbance of *M. graminicola* and *M. sicula*, even though the latter's cryptic habits and narrow distribution

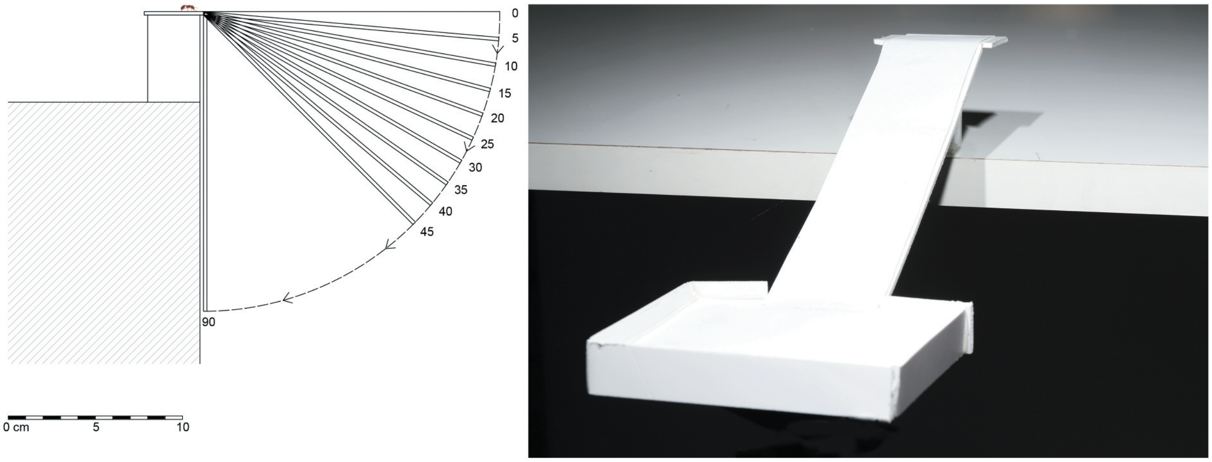

Figure 1. Experimental setup used for the sloped plane test. During the experiments, the ant walked descending the sloped plane, whose inclination could be set at different angles.

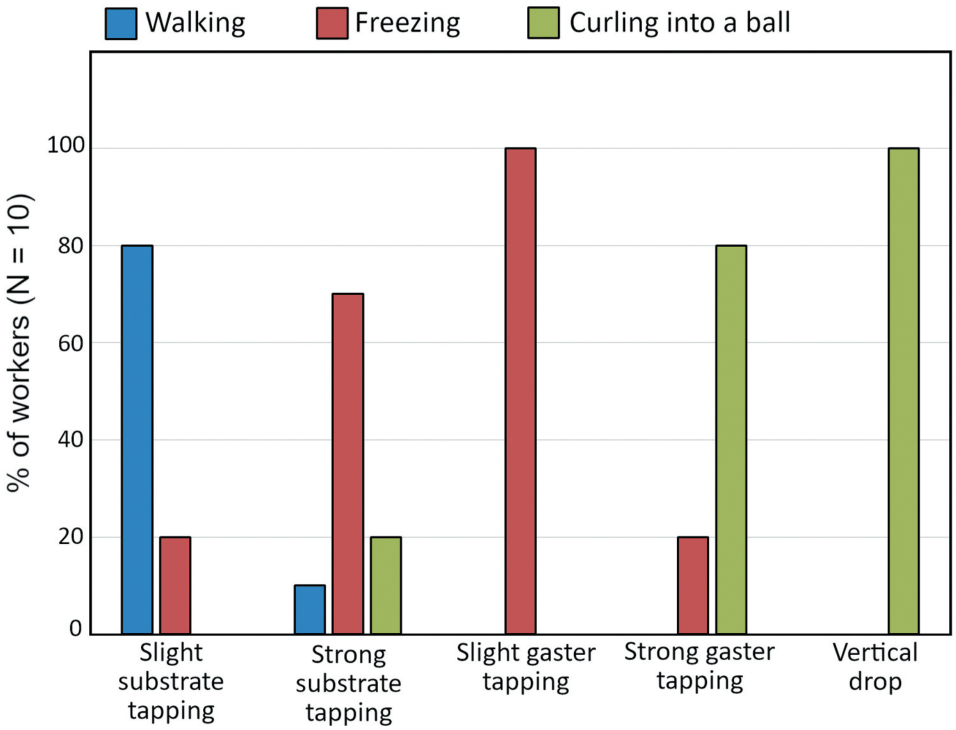

Figure 2. Behavior of *M. sicula* workers in response to different stimuli on the horizontal plane.

Figure 3. On the left, a worker of *Myrmecina graminicola*, assuming its characteristic ball-like position. On the right, a worker of *M. sicula* walking (above) and curling into an imperfect ball-like position (below). Scale bars: 1 mm.

make it more difficult to study. In comparison to *M. graminicola, M. sicula* adopted a partly overlapping set of behavioral responses: frequent freezing, and, under stronger stimuli, curling into a ball-like shape. These may hypothetically be considered defensive mechanisms against some attackers, but this can only be established through observations of more realistic interactions against predators or other ants. However, unlike *M. graminicola*, the ball-like shape of *M. sicula* was less refined, lacking the quick retraction and complete adherence of the appendages to the body. Moreover, a ball-like position was remarkably never assumed when ants were disturbed on inclined surfaces but only when workers were physically detached from their substratum. The ability to form a better ball-like shape is

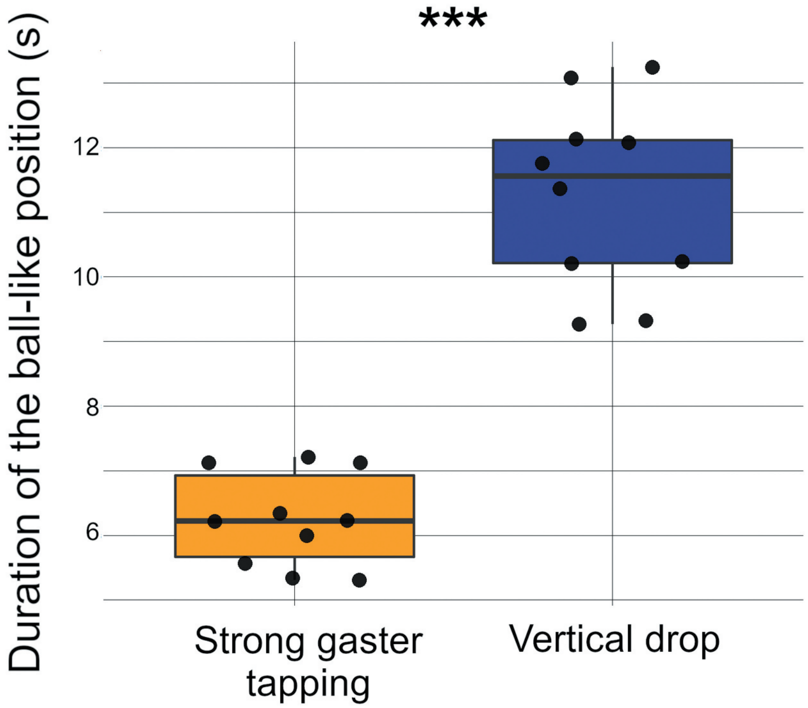

Figure 4. Duration of the ball-like position of *M. sicula* ants on the horizontal plane recorded in response to strong gaster tapping and vertical drop respectively (N = 10 for each box).

essential to allow *M. graminicola* to roll away effectively, and its ability to quickly react to disturbance by actively rolling away is a remarkable defensive strategy (Grasso et al. 2020). While it is possible that the "imperfect" ball-like shape rarely assumed by *M. sicula* upon a very strong disturbance may lead to a passive form of rolling, it is clear that *M. sicula* does not exhibit the same escape strategy of *M. graminicola*: it may only roll away if it assumes a ball-like shape when something makes it lose contact from the substratum, while *M. graminicola* actively makes a kick-like movement against the substratum to propel itself (after assuming its more refined ball-like shape). However, this behavior may be a distant relative to that of its actively rolling congener.

Physical characteristics of *M. sicula* may play a role in its lack of a developed rolling behavior. In particular, *M. sicula* is averagely smaller than *M. graminicola* and its scapi have a different shape (Schifani et al. 2020). Whether the different shape of the scapi has any direct influence on the ability to retract them close to the head is unclear. In addition, *M. sicula* tends to live in different ecological conditions in terms of microhabitats compared to *M. graminicola*, which may be relevant to the adaptive value of a rolling strategy. *Myrmecina graminicola* appears to have a strong preference for broadleaved woodlands, where it forages on the leaf litter (Seifert 2018; Schifani et al. 2020). Dead leaves of broadleaved plants are considered ideal inclined surfaces on which rolling is highly efficient (Grasso et al. 2020). On the contrary, *M. sicula* is more frequently recorded in sparsely vegetated habitats such as shrublands (>20% of documented sites) and grasslands (>30%), or in artificial pine forests (>20%) (Schifani et al. 2020), which may not offer the same opportunities. Finally, it is worth noting that *M. sicula* has a smaller eye to head size ratio compared to *M. graminicola*, which is an hypothetical indication of a more endogean foraging activity (Schifani et al. 2020), and attempting to roll away from a predator may be ineffective or unfeasible in endogean microspaces. The other W-Palearctic species, *M. atlantis* Santschi, 1939 and *M. melonii* Rigato, 1999, are similar to *M. sicula* in all the aforementioned characteristics (Rigato 1999; Schifani et al. 2020).

Behavioral and phylogenetic data on a larger number of species will be needed to understand the evolutionary pathways leading to the development of the unique rolling behavior of *Myrmecina* ants, and comparative morpho-functional analyses may be useful to better understand its biomechanical requirements.

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Supplementary material

Supplemental data for this article can be accessed here

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